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The Use of Human and Conspecific Gestures By Capuchin Monkeys to Solve an Object-Choice Task

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The use of human and conspecific gestures by capuchin monkeys to solve an object-choice task

By

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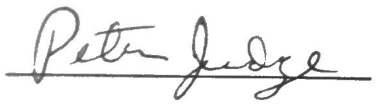

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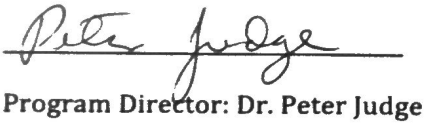

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Abstract

Most primates live in highly complex social systems, and therefore have evolved similarly complex methods of communicating with each other. One type of communication is the use of manual gestures, which are only found in primates. No substantial evidence exists indicating that monkeys use communicative gestures in the wild. However, monkeys may demonstrate the ability to learn and/or use gestures in certain experimental paradigms since they've been shown to use other visual cues such as gaze. The purpose of this study was to investigate if ten brown capuchin monkeys (*Cebus apella*) were able to use gestural cues from monkeys and a pointing cue from a human to obtain a hidden reward. They were then tested to determine if they could transfer this skill from monkeys to humans and from humans to monkeys. One group of monkeys was trained and tested using a conspecific as the cue giver, and was then tested with a human cue-giver. The second group of monkeys began training and testing with a human cue giver, and was then tested with a monkey cue giver. I found that two monkeys were able to use gestural cues from conspecifics (e.g., reaching) to obtain a hidden reward and then transfer this ability to a pointing cue from a human. Four monkeys learned to use the human pointing cue first, and then transferred this ability to use the gestural cues from conspecifics to obtain a hidden reward. However, the number of trials it took for each monkey to transfer the ability varied considerably. Some subjects spontaneously transferred in the minimum number of trials needed to reach my criteria for successfully obtaining hidden rewards ($N = 40$ trials), while others needed a

large number of trials to do so (e.g. $N = 190$ trials). Two subjects did not perform successfully in any of the conditions in which they were tested. One subject successfully used the human pointing cue and a human pointing plus vocalization cue, but did not learn the conspecific cue. One subject learned to use the conspecific cue but not the human pointing cue. This was the first study to test if brown capuchin monkeys could use gestural cues from conspecifics to solve an object choice task. The study was also the first to test if capuchins could transfer this skill from monkeys to humans and from humans to monkeys. Results showed that capuchin monkeys were able to flexibly use communicative gestures when they were both unintentionally given by a conspecific and intentionally given by a human to indicate a source of food.

Introduction

Communication in both wild and captive primate societies has been well documented. Primates have many modes of communication in order to relay signals about food, sex, aggression, other primates, and other animals. Most primates live in highly complex social systems, and therefore have evolved similarly complex methods of communicating with each other. Diverse modes of communication among primate societies show how the act of communicating in groups is necessary in many different contexts. Communication is necessary to maintain social relationships by mediating interactions, avoiding conflict, and affiliating with others, as well as for avoiding predators and communicating with other groups (Strier, 2011).

The necessary components of communication include a signal, motivation, and meaning. The signal is an act of communication, motivation refers to the sender's internal state, and the meaning is an expression of what the recipient perceives the signal to be. Altmann (1967) states that the definition of communication cannot be restricted to the signals, or to the response to the signals, but is a "process by which the behavior of an individual affects the behavior of others." Living in social groups is beneficial as it allows for an increase in foraging efficiency and anti-predator behavior (Strier, 2011). Therefore, a system of communication in groups can be adaptive. However, in order for such groups to evolve some form of communication must occur. The four main modes of primate communication are tactile, olfactory, vocal, and visual.

Many primate societies exhibit high amounts of physical contact in their daily lives. Groups often come into physical contact while grooming or playing. For years,

infants cling to their mothers' backs and aggression is often displayed as bites, scratches, and pushes. Reconciliation after a fight can be exhibited in the form of touching and other affiliative behavioral responses. Tactile communication is also necessary for copulation, and sometimes courting (Strier, 2011).

Primates also have a wide range of auditory signals that are used for many different purposes. Such signals are especially useful for primate species that live over large ranges or that live in dense habitats, such as rainforests (Altmann, 1967). Vervet monkeys (*Chlorocebus pygerythrus*), which live in the savannahs of Africa, exhibit a large repertoire of different signals depending on whom they are communicating with. They give different calls in intergroup and intragroup interactions, as well as in response to different types of predators (Zuberbuhler, Noe, & Seyfarth, 1997). Within groups, primates often have a range of agonistic and affiliative encounters, many of which are accompanied by vocal signals. Some calls are given when an individual is attacked, and therefore may function as a defensive threat or a solicitation to others for help (Altmann, 1967). Some females also exhibit anti-copulatory calls to ward off males when they are not in estrus. Between groups, primates may use vocal communication to defend their territories or monopolize a food source (Altmann, 1967).

Olfactory communication involves odorants that can be sensed in the presence of another animal, or deposited and left behind by an animal. These scents could be pheromones that are deposited by glands that exist on different body surfaces, often on the anogenital region. Such signals can convey the reproductive status, age, identity and sex of an individual (Strier, 2011). Often, olfactory cues are used in combination with

other types of communication; therefore, cues are often not direct or immediate (Altmann, 1967).

An advantage of visual communication is that it allows for the transfer of a signal between individuals without a tactile connection (Snowden, Brown, & Petersen, 1982). Terrestrial primates make great use of visual communication as they usually live in more open landscapes and can see each other. Visual communication is often categorized into passive and active communication. Passive communication refers to visual signals such as color, hue or size. Adult male patas monkeys (*Erythrocebus patas*) have white fur around their posterior, which can act as a signaling function for its social group (Altmann, 1967). Active communication, such as the use of facial expressions, is often also used in primate societies as a method of communication. One example is lip smacking, which is a nonaggressive expression exhibited by both dominant and subordinate individuals (Altmann, 1967).

Another type of active visual communication is the use of manual gestures, which are only found in primates (Roberts, Vick, & Buchanan-Smith, 2012). They have been defined as a non-locomotory movements of a finger, wrist, hand, foot, leg, or arm that is directed towards another individual and has communicative value (Pollick & de Waal, 2007). The use of manual gestures has been documented in apes such as chimpanzees (*Pan troglodytes),* bonobos (*Pan paniscus)*, and gorillas (*Gorilla gorilla)* in both the wild and captivity (Pollick, & de Waal, 2007, Roberts et al., 2012, Genty, Breuer, Hobaiter, & Byrne, 2009, Hopkins & Leavens, 1998). Apes use gestural signals in the contexts of playing, grooming, sexual activity, aggression, affiliation, and feeding (Pollick & de

Waal, 2007). Many gestures can be used in one context but for a variety of different goals, and a single gesture may also serve more than one purpose or goal (Hobaiter & Byrne, 2011). For example, a gesture that indicates a desire to copulate with a female may also function as a warning to other males to stay away (Hobaiter & Byrne, 2011). An ability to use gestural cues of different types could be adaptive in the highly communicative societies in which most primates live. Although apes use communicative gestures in the wild, there is no substantial evidence that monkeys use intentional communicative gestures in the wild (Tomasello & Zuberbühler, 2002). However, this does not necessarily mean that they do not have the ability to learn and/or use gestures in certain experimental paradigms.

Some primate species have been shown to use unintended visual behavioral cues, such as facial expressions. Research has shown that marmosets (*Callithrix jacchus*) are able to use the facial expressions of conspecifics shown on a screen as a social reference to determine whether or not a certain food is attractive (Kemp & Kaplan, 2013). Similarly, capuchin monkeys modified their duration and frequency of reaching towards a container after witnessing differential facial expressions directed towards the container (Morimoto & Fujita, 2011). Different primate species have also been shown to use the gaze of a conspecific as a reliable cue. Tomasello, Call, & Hare (1998) investigated the ability of five different primate species to follow the gaze cue of conspecifics. The species tested were chimpanzees, sooty mangabeys (*Cercocebus atys torquatus*), rhesus macaques (*Macaca mulatta*), stumptail macaques (*Macaca arctoides*), and pigtail macaques (*Macaca nemestrina*). Experimental trials consisted of the experimenter

holding up an orange so that one individual looked at it, and recording if another individual followed the gaze to the orange. They found that all five primate species were able to follow a clear gaze cue from a conspecific in over 80% of the trials. This study suggests that different primate species are able to pick up unintentional cues such as gaze.

A study by Mason and Hollis (1962) tested rhesus monkeys in an object choice task, in which they had to use cue information from a conspecific informant to find a hidden reward. They found that subjects were successful in using information from the informant, but did not specify the cues they used. Subjects were also tested with a monkey puppet and a plaque as a cue giver. Both objects were placed in front of the cart containing the food item, and their location was meant to be the cue. Most of the cues from the monkeys included the informants' positioning near the reward, but the authors state that position alone was probably not a salient enough cue as subjects did not do as well when the monkey puppet, or plaque, was placed in front of the correct reward. The study determined that while training the subjects to use the informant's cue took over one thousand trials, they were able to transfer their use of the cue when presented with a new conspecific informant. Since primates have been shown to use gaze cues and positioning cues to solve object choice tasks, they may be able to use additional cues from others to solve certain tasks as well.

We know animals are capable of reading cues because many animals have been shown to be able to interpret gestural cues given by humans. Smet and Byrne (2013) tested African elephants (*Loxodonta africana*) on their ability to use a human-given point to find hidden food in an object choice task. The experimenter would point to one of two

containers containing the food, and the elephant would be allowed to select its choice. The study used conditions including the experimenter standing centrally, or closer to the wrong or correct container. The arm used was also varied between the ipsilateral and contralateral in relation to the correct location of the food. The study found that the elephants were able to use the point cues to obtain food significantly above chance in all conditions. They did even better when the experimenter was also standing near the correct container, showing that the elephants were also using body location in their decisions. Another study tested identically raised domesticated dogs (*Canis familiaris)* and wolves (*Canis lupus)* on a similar task (Virányi, Gácsi, Kubinyi, Topál, Belényi, Ujfalussy, Miklósi, 2008). They found that dogs and wolves were able to successfully use a human pointing cue to find hidden food, though the wolves' performances were relatively poor and varied highly. The authors suggest that differences between dogs and wolves may arise as a result of traits selected for during domestication. Clark's nutcrackers (*Nucifraga Columbiana)* were also tested on an object choice task to obtain hidden food (Tornick, Gibson, Kispert, & Wilkinson, 2011). They were given human cues such as touching the correct container, pointing to it, or gazing at it. Five out of six of the subjects tested were able to use each cue to find the hidden food.

As many species read human cues, it is not surprising that apes and monkeys also have the ability to use human given cues to solve object choice tasks. In captivity, both monkey and ape species have been able to learn to use cues to solve such a task. In an object-choice task, one of two opaque containers is baited with food out of sight of the subject animal. The subject is then allowed to see the two containers and the

experimenter or conspecific indicates the correct choice. The subject then gets the opportunity to choose between the two containers, and receives the reward if it chooses correctly. These cues are usually limited to a gaze cue plus a movement such as pointing, sometimes combined with a vocalization. A study by Itakura & Tanaka (1998) discovered that chimpanzees were able to successfully use a human gaze and head orientation cue from a distance of 15cm and 60cm in an object choice task. The chimpanzees were also able to use a glance from just the eyes of the experimenter, but they took more trials to do so successfully. An orangutan (*Pongo pygmaeus*), was also tested, and was 100% successful using the same cues as the chimpanzees except glancing, for which she made a single error. This orangutan, however, was a show orangutan working with her trainer as the experimenter. Therefore, it is possible the orangutan had learned to use gazing and/or glancing cues in previous unrelated training. Another study by Peignot and Anderson (1999) demonstrated that gorillas were able to use gaze cues from human experimenters. When presented with an object choice task and cues from a human experimenter, they were successful in almost every condition. These conditions included a "close" and "far" gaze and head orientation cue. However, in the condition of only eyes gazing, without the head orientation, at the correct container, the gorillas' performances were unsuccessful. Thus, the great apes are able to use head orientation and gaze cues together to solve object-choice tasks, but perform with less success when given only an eye-gaze cue. Anderson, Sallaberry, and Barbier (1995) tested capuchin monkeys in a similar task that used both human gaze and pointing cues towards a hidden reward. In this experiment a gazing cue, as well as other cues, were

used to indicate where food was located in an object-choice paradigm. The only experiments in which the capuchins tested above chance were those that involved pointing cues. This suggests that cues other than gaze, such as pointing, are also necessary for capuchin monkeys to make use of the cue.

Povinelli, Parks, & Novak (1992) trained rhesus monkeys as informants or cue-givers as part of a study that investigated their ability to transfer knowledge of a task across roles played in a trial. In order to train monkeys as informants, they sat opposite a human experimenter and were rewarded when they made any manual gestures towards the location of food that was hidden from the human. All monkeys were able to learn to provide a reaching gesture in order to receive a reward. Baboons have also been taught to use a manual 'pointing' gesture through operant conditioning (Meunier, Prieur, & Vauclair, 2013). Povinelli, Nelson, & Boysen (1992) also conducted this study with chimpanzees and were able to train subjects to use a manual gesture to indicate the location of a hidden reward. These results show that it is possible for apes and monkeys to provide reliable cues to indicate the location of hidden food. Another study on chimpanzees tested to see if they were able to understand pointing cues given by both a human and a conspecific (another chimpanzee) towards a hidden piece of food (Itakura, Agnetta, Hare, & Tomasello, 1999). Chimpanzees were given an object choice task, and expected to use cue information to make their decision. The first cue given was a local enhancement cue, in which either a human or another chimpanzee stood next to the correct bucket of food. The second cue was a gaze and point cue, also given by a human, and then another chimpanzee. The study found that the chimpanzees performed better

when the human or chimpanzee stood next to the hidden food rather than only pointing at the food. In the second part of the study, they added a vocal cue. The experimenter gave a gaze cue with a simulated 'chimpanzee bark' or a nonsense word. The chimpanzees did significantly better with vocalizations, but results between the two vocalizations were similar. This suggests that other cues may be necessary for chimpanzees to detect the presence of a reward using gestural cues. In the wild, many chimpanzees may detect the location of food based on the proximity of another ape to the food. Therefore, they may need a more robust cue than a point to detect the presence of food. Another study found that a gaze cue alone was not sufficient, and that a vocalization, or a gestural movement was also necessary for chimpanzees to read the cues from humans (Call, Agnetta, & Tomasello, 2000). The sounds included in this study were a simulated chimpanzee bark made by the experimenter, snapping the fingers, and slapping the table. However, gestural movements were not made in the direction of the hidden food. Rather, only a gaze cue was given, and the sounds were used in order to draw the attention of the subject to the cue giver.

The purpose of this study was to investigate if brown capuchin monkeys were able to use gestural cues from monkeys and a pointing cue from a human to obtain a hidden reward, and then transfer the skill between species. Because capuchin monkeys have exhibited the ability to learn to use pointing cues from a human experimenter (Anderson, Sallaberry, and Barbier 1995), we hypothesized that they could learn to use gestural cues from conspecifics in the same type of object choice task. To date, there are no studies that test capuchin monkeys' (*Cebus apella)* abilities to use a conspecific's

gestural cues in an object-choice task. Subjects at Bucknell University's Animal Behavior Lab were tested on this task and a human pointing task. I tested two groups of monkeys in an object-choice paradigm using cues from either a human experimenter or a conspecific. The first group of monkeys was trained and tested using a conspecific as the cue giver. Once these trials were completed, the subject monkeys were then tested with a human experimenter. The second group of monkeys began training and testing with a human cue giver, and later moved on to a monkey cue giver. If the monkeys were able to learn the skill with conspecifics, I was able to test if they were able to transfer this skill to the human experimenter, and vice versa. In both cases, the subject monkey should take fewer trials to achieve over chance performance with the second species giving them cues if they were flexibly using the gestures as a form of communication. To date, there are no studies that test the transfer of using a cue from one species to another. While Itakura et al. (1999) tested chimpanzees on an object-choice task using cues from both conspecifics and humans, they did not analyze the possibility that the chimpanzees learned to use the skill from the conspecifics and then used this knowledge to understand a cue from the human. They were also not able to test some chimpanzees first with human cue givers, and therefore could not make the same comparisons made in this study.

In this study subjects sat in an apparatus that allowed them to see another monkey or a human cue giver, but kept them physically separate. A pair of inverted opaque cups was placed in between the subject and the conspecific or human. One cup was baited out of sight of the subject. Depending on the condition, the subject then watched the

conspecific make a gestural cue towards the baited cup, or the experimenter point to the cup. The cups were then moved within reach of the subject, who was allowed to turn one of the cups to see if a reward was inside. If the subject used gestural cues, it should select the cup that the gesture indicated, and therefore would receive a reward.

I predict that successful performance demonstrates flexible communicative cognitive abilities in capuchin monkeys. Capuchin monkeys were not only able to read cues given by others even though they do not naturally use gestural communication, but that they can do so from two different species. Secondly, they were able to transfer this knowledge between species, and test at above-chance levels more quickly when moved to the second species. Thirdly, if monkeys failed to use cues given by one species, they were tested on their ability to use cues from the other species. There have been no other studies conducted of this kind. This study contributes the first data on whether capuchin monkeys can use gestural cues from one species, and transfer the cue use to the other species. Results show that capuchin monkeys are able to flexibly use communicative gestures when they are both unintentionally given by a conspecific and intentionally given by a human to indicate a source of food.

Methods

Subjects and Housing

Ten brown capuchin monkeys (*Cebus apella*), two adult males, five adult females, and three juveniles, participated in the experiment. Subjects were socially housed in a group of 17 individuals that consisted of two adult males, nine adult females, four

juveniles, and two infants. The colony was established in 2000, and the dominance hierarchy of its members has remained stable since. No other animals have been introduced or removed from the colony other than by birth or death. All monkeys that would reliably enter the apparatus, were not infants, or whose infants did not physically interfere with the testing situation, were chosen to participate. Cueing monkeys were two adult males and six adult females. Subjects and cueing monkeys were paired together if there were no excessive threats or distractions made by one of the two monkeys when they faced each other in the apparatus. Such threats or distractions were considered excessive if one of the monkeys would not reliably stay in the apparatus. Subjects randomly assigned to the conspecific-first group were Monet (Mt), Socrates (Sc), Schroeder (Sd), Niko (Nk), and Newton (Nw). The remaining subjects in the human-first group were Nye (Ny), Davinci (Dv), Sheba (Sb), Smithson (Sm), and Stella (St). Cueing monkeys were Nobel (Nb), Deangela (De), Davinci (Dv), Monet (Mt), Newton, (Nw), Niko (Nk), Socrates (Sc), and Schroeder (Sd). Cueing monkeys were assigned to subjects randomly, and only switched if the cueing monkey would not give reliable cues or the subject monkey would not reliably stay in the apparatus when the cueing monkey was present. None of the subjects had experience with object-choice tasks, although some subjects were familiar with the testing environment from previous studies.

Subjects were housed in the Animal Behavior Laboratory at Bucknell University, Lewisburg PA. Housing consisted of caging that spanned three separate rooms, with compartments interconnected by doorways and overhead tunnels (Figure 1). The doorways could be closed, and the tunnels blocked with metal barriers, in order to

separate animals into separate compartments. There were 17 possible subcompartments that could be closed off, three of which were used for testing. Compartments were furnished with perches, platforms, and swinging toys to allow for naturalistic movement. Floors were made of linoleum and covered with wood shavings. Subjects were fed twice a day on a diet of monkey chow, cereals, nuts, grains, fruits, and vegetables. Water was available ad libitum. Daily enrichment was provided for all monkeys in the form of toys and climbing structures. Participation in research was also considered enrichment for this group. All procedures were approved by Bucknell's Institutional Animal Care and Use Committee according to requirements within the Guide for the Care and Use of Laboratory Animals.

Apparatus

Three rooms, two large rooms connected by a central smaller room, in the capuchin enclosure were used for testing (Figure 1). The larger side rooms measured 1.6 by 2.2 by 2.4 m and the smaller middle room measured 0.9 by 1.0 by 0.5 m. There were openings measuring 0.6 by 0.6 m, 0.9 m from the ground, in the walls connecting the three rooms. The apparatus consisted of a rectangular steel frame measuring 0.6 by 1.1 by 0.5 m. The apparatus was placed in the openings interconnecting the three rooms and spanned the length of the middle room (Figure 2). Wire caging segmented the apparatus frame into three sections. The two side sections allowed for monkeys to enter and sit in the apparatus through the openings in the wall. The center compartment of the apparatus held a 43.2 cm bar that slid back and forth between the two side sections. On each end of the bar was an inverted white cup with one side cut out that was able to swivel 360˚. The

holes in the caging wire (2.5 x 5 cm) entering into the center section of the apparatus were large enough for the monkeys to reach the length of their arm into the center compartment to access the cup, and for a human experimenter to extend an entire index finger through the caging.

Procedures

Training. Training consisted of four phases that were meant to accustom the subjects to the apparatus and the nature of the experiment. Half of the subjects went through training with a conspecific, while half went through training with a human experimenter (E). The following depicts the training phases in which the cue giver was a monkey or a human, depending on the testing group in which the subject belonged. Either a single experimenter, or two experimenters stood next to the apparatus in order to move the cups from the cue giver to the subject.

Phase 1. Phase 1 trained the subjects to properly turn the cups on the bar in the center portion of the apparatus order to retrieve a reward (Figure 3a). The subject watched E bait one cup, and was then given the option to take the reward from the cup. The angles of the cups increased from 0˚ to 90˚, 120˚, and 180˚ away from the subject. Subjects were required to consistently turn the baited cup to retrieve the reward even though it eventually could not see the reward at a 180˚ angle. The subjects were given five trials at each angle for a total of 20 trials.

Phase 2. Phase 2 trained the subject monkey that the cue giver was able to retrieve a reward from the cups (Figure 3b). The cups were oriented so that the open side

faced the subject monkey. Both the subject and cue giver watched the baiting process, and the cups were then moved towards the cue giver. The cue giver turned the cups to retrieve the reward. Subjects were given two blocks of 10 trials in this phase.

Phase 3. Phase 3 trained the subject that the cue giver could see and retrieve the reward, even when the subject could not see the reward in the cup (Figure 3c). Therefore, the cue giver should be considered an informed partner. The cups were oriented so that the open side faced the cue giver. Both the subject and cue giver watched the baiting process. The cups were then moved towards the cue giver, who retrieved the reward. Thus, even though the subject could not see the reward in the cup, it could see that the cue giver was able to see it and retrieve it. Subjects were given two blocks of 10 trials at this phase.

Phase 4. Phase 4 trained the subject that the cue giver was able to see and retrieve the reward when the subject did not witness the baiting process, and was therefore still an informed partner (Figure 3d). The cups were oriented so that the open side faced the cue giver and the baiting process was hidden from the subject by a 0.7 by 0.4 m wooden board. When the board was removed, the cups were moved toward the cue giver who retrieved the reward. Though the subject could not know that there was a reward in one of the cups, it saw that the cue giver was still able to see the reward and take it. Subjects were given four blocks of 10 trials at this phase.

In total, 100 trials were given across all training phases for each subject. In phase 1 the rewards alternated between the two cups between each trial. In phases 2-4 the

rewards alternated in a pseudorandom order in which the reward was in each cup five times in one block of 10 trials, and never in the same cup more than twice consecutively.

After the cue giver received the reward in each training trial, a reward would be placed in the same cup for the subject monkey in order to maintain its interest in participating. When two experimenters were present with the apparatus, baiting was alternated between the two to avoid bias for one experimenter. When only one experimenter was present with the apparatus, the experimenter spent the first five trials on one side of the apparatus, and the next five trials on the other side of the apparatus. The side on which the single experimenter started was alternated at every block of trials. This was done so the position of the experimenter did not introduce any bias into the experiment.

Testing Conditions. There were three conditions used in this study, *conspecific, pointing,* and *control.*

Conspecific. In this condition, the subject would sit opposite another monkey and use any cues given by a cue giver monkey to choose a cup. Cues included extending the arm through the cage wiring from a finger to the entire arm, as well as sitting in front of the baited cup and gazing into it. All cues occurred, but cues using any sort of limb extension through the wire caging were considered the most obvious.

Pointing. In this condition, the subject would sit opposite a human experimenter (E). E would slowly lift the arm on the same side of the baited cup, and then extend the arm and index finger completely forward through the caging at the level of the cup and on the same side. E would alternate her eyes between the subject and the reward.

Control. In this condition, there would be no cue giver. One cup was baited out of view of the subject. The cups were then moved towards the subject without a cueing monkey or pointing human across from it. Control trials were used to create a baseline of success for each subject without using cues. They were also used to ensure that subjects were not using inadvertent cues from the experimenters that were standing next to the apparatus and moving the cups to determine the correct cup and obtain rewards.

Test Trials. Trials began with boards blocking the view of both the cue giver and the subject (Figure 4). In order to maintain the cueing monkey's interest in participating, a trial began by first rewarding the cueing monkey. One cup was baited, the board on the cueing side was then removed, and the cups were moved to the cue giver. If the cue giver was a monkey, it received the reward and the cups were re-baited for the testing trial. If the cue giver was E, the reward would remain in the cup. If a human was cueing, this trial was done so the time in between trials was consistent, and so the trials were the same as trials with a conspecific cue giver. This 'cueing monkey reward' portion of a trial was also done before each control trial to maintain consistency in timing. A test trial for the subject was then given immediately after. One cup was baited, and both boards were removed. The cups were slid towards the cue giver, who would give a cue that differed depending on whether the cue giver was a monkey or a human. After the cue was given, the cups were quickly moved to the subject monkey. The subject monkey would make a choice by rotating one of the cups. If it chose the cup that contained the reward it was allowed to retrieve the reward. If it chose the wrong cup, the reward was moved out of reach and the correct cup was turned to show the subject the location of the reward.

Testing was conducted five days a week from January 2012 until March 2014. Each subject was given a maximum of 10 trials per day. Sessions lasted about 5-7 minutes per monkey.

In order to accurately compare the use of conspecific cues and human cues in the test condition, half of the subjects were trained starting with a conspecific, and half were trained starting with a human experimenter. For the conspecific conditions, monkeys were tested with at least two different conspecifics as cueing monkeys to test for transfer across conspecifics. The human experimenter remained constant for each subject monkey.

A binomial test was used for each subject to test for deviation from the expected outcome of performing at chance levels. The criteria was 17/20 correct, which had a probability of $p<.05$ according to a binomial distribution. Therefore our criteria for success in any of the conditions was to obtain 17 out of 20 trials correct in two consecutive ten trial sessions, and then to repeat that 17 out of 20 trial success in the next two ten trial sessions. This was to ensure our criteria was very conservative.

The general testing procedure for the conspecific-first group was to test the subject in the conspecific condition first, and then in the pointing condition. In the human-first group, subjects were tested in the pointing condition first, and then the conspecific condition. If subjects failed the first condition, they were still tested in the second condition. A subject was considered to have failed if it exhibited a side bias, in which it picked the same cup on every trial, for at least 100 trials. If the subject chose at random for 100 trials and therefore did not succeed at getting more than 50% of the trials

correct on average, it was also considered to have failed. This ensured that all subjects were tested with both a conspecific and a human experimenter. If subjects failed their first condition, but later became successful in the second condition, they were retested in the condition in which they had previously failed. For example, if a subject failed in the conspecific condition but was successful in the pointing condition, it would be retested in the conspecific condition.

Results

All of the subjects in each condition went through every training phase. In the conspecific-first group, two of five subjects reached the criterion for success in both conspecific and human trials. The minimum number of trials required to be considered successful in any condition was 40, since my criteria required subjects to get 17/20 trials correct twice consecutively. Each subject's success across all conditions is shown in Table 1. Sc was tested with four conspecifics and reached criterion within 140 trials with her first cue giver, within 40 trials with her second cue giver, and within 100 trials with her fourth cue giver. This showed her ability transfer the use of the cue across conspecifics. She was not successful with her third cue giver, an adult male, probably because he only provided a gaze and not more obvious cues such as reaching. When tested with the second male who provided reaching cues she was successful. She was then tested in the human pointing condition and reached criterion within 60 trials. This was evidence of her ability to transfer the use of the cue from conspecifics to humans because it took many more trials (N=140) to learn to use the cue from the first

conspecific (Figure 5). Nw was tested with three conspecifics and reached criterion in 190 trials with her first cue giver, 100 trials with her second cue giver, and 140 trials with her third cue giver. Results showed no transfer of the skill across conspecifics. She was then tested in the human pointing condition and reached criterion after 190 trials. Results showed no transfer of the skill from conspecifics to humans (Figure 6).

Three of five subjects were not initially successful in either the conspecific condition or in the human pointing condition. Call et al. (2000) showed that the use of vocalizations in an object-choice task helped increase the performance of some chimpanzees. A vocalization cue can be helpful because it can draw the attention of the subject to the cue giver, and because many primates use vocalizations in the context of finding and eating food (Call et al*.,* 2000. Itakura et al*.*, 1999). I therefore added a third condition, which was identical to the human pointing condition but with an added vocalization, called the vocal point condition. The trial was the same, except the experimenter would say "this one" when pointing to the baited cup.

Sd was first tested with two conspecifics and then in the pointing condition but did not reach criterion. She was then tested in the vocal point condition and reached criterion in 200 trials. She then reached criterion in 40 trials when retested in the pointing only condition and in 40 trials when retested in the conspecific condition (Figure 7). Results indicated that Sd was able to transfer the use of the skill from the vocal point trials to the pointing trials, and from human pointing trials to conspecific trials. Nk was first tested with two conspecifics and then in the pointing condition but did not reach criterion. She was then tested in the vocal condition and reached criterion in 170 trials.

She then reached criterion in 40 trials when retested in the pointing only condition, indicating transfer of the use of the point. She reached criterion in 150 trials when retested in the conspecific condition, which indicated that she did not transfer using a cue from a human to a conspecific (Figure 8). Mt was tested with two conspecifics, in the pointing condition and in the vocal point condition, but did not reach criterion in any condition (Figure 9).

In the human-first group, two of five of the subjects reached criterion in both the human pointing and conspecific condition. St was successful in the first pointing condition within 130 trials. She was then tested in the conspecific condition and reached criterion in 40 trials with her first cue giver and in 40 trials with her second cue giver (Figure 10). Results showed that she was able to spontaneously transfer the ability to use the cue from a human to a conspecific, and across conspecifics. Ny began testing in the pointing condition and reached criterion within 140 trials. He was then tested in the conspecific condition and reached criterion within 110 trials with the first cue giver and within 40 trials with the second cue giver (Figure 11). Results indicated that Ny was not able to transfer the use of the cue from a human to a conspecific cue-giver, but was able to do so across conspecifics. Dv was unsuccessful in the pointing condition, and then unsuccessful in the conspecific condition with two different conspecifics, and so was advanced to the vocal point condition. He was successful in the vocal point condition within 180 trials. He was then retested in the pointing condition and was successful within 40 trials. Results indicated that he was able to transfer the use of the skill from the vocal point condition to the pointing condition. When retested in the conspecific

condition he was unsuccessful in 150 trials and was no longer tested (Figure 12). Sm was unsuccessful in the first pointing condition. He was then tested in the conspecific condition and was successful in 80 trials (Figure 13). In future testing, Sm will be retested in the pointing condition to see if he is able to transfer the use of the skill from a monkey cue giver to a human cue giver. Sb was unsuccessful in her first pointing condition ($N = 220$ trials), and vocal point condition ($N = 100$ trials; Figure 14). In future testing, she will be tested in the conspecific cueing condition. The order in which Sb was tested was different than the rest of her group, as she received the pointing condition, followed by the vocal point condition. This was done to see if following the pointing condition immediately with the vocal point condition, instead of the conspecific condition, affected her performance.

Discussion

Results showed that capuchin monkeys could learn to use a conspecific gestural cue and a human point to solve an object choice task. Monkeys were also able to transfer their use of a cue between species, though there were many individual differences in their ability to do so. Six animals were able to use a conspecific cue and a human point, transferring the skill between two species. However, the order in which they completed the conditions and learned the skill varied across subjects.

Three animals learned to use one type of cue, and then spontaneously used this knowledge when presented with another species of cue giver (human vs. monkey). All of these animals took much longer to learn the skill initially, but transferred the skill when

presented with a novel cueing condition. Other animals had to relearn the skill entirely from the new type of cue giver. For example, in the conspecific-first group Sc and Nw were the only two to learn to use the conspecific cue first. However when switched to the human pointing condition, Sc quickly transferred the ability and used the human cue (60 trials), but Nw took 190 trials to learn to use a human cue. The number of trials was the same as it took her to initially learn to use a conspecific as a cue giver ($N = 190$). The number of trials it took to transfer the ability between conspecifics also varied for both subjects (Sc=40, 100; Nw= 100, 140). Results indicated that Sc was faster at transferring the ability to read the cue or point between species, and to read the cue between two conspecifics than Nw. Sc learned to use the gestural cue of a conspecific and used this previous knowledge to understand and interpret a human pointing at the baited cup. Nw showed the opposite pattern, of needing to relearn the new type of cue. A similar trend was shown in the human-first group, in which St and Ny first reached criterion in the pointing condition, and then reached criterion in the conspecific condition immediately after. St was successful in learning to use the human point within 130 trials, and directly transferred this ability to the conspecific cueing condition, reaching criterion in the minimum 40 trials. Ny was successful in learning to use the human point in 140 trials, but took another 110 trials to reach criterion in the conspecific cueing condition. Results indicated that St was able to spontaneously transfer the ability to use a cue across conditions, while Ny more likely relearned to use a conspecific gestural cue when introduced to that condition. Theoretically, the spontaneous transfer of the use of a human pointing cue to a conspecific gestural cue, or vice versa, could mean that capuchin

monkeys were able to learn to read another's behavior to find food, and then use this information even when it came from another monkey or another species.

Two of the monkeys initially learned to use a cue in the vocal point condition and then transferred it to a human point and conspecific cue. Though Sd and Nk were in the monkey-first group, they did not learn to use any cue until the vocal point condition. They learned to use a human point first, and later transferred that to the conspecific-cueing condition. Both of these subjects were able to transfer their ability to use the vocal point cue to using only a pointing cue. However, both of these subjects varied in their ability to transfer the use of a human-given cue to a conspecific-given cue. While Sd did so immediately, reaching criterion in the minimum 40 trials, Nk took 150 trials to do so. Nk probably relearned to use the conspecific cue in the same way that she learned to use the human-given point, while Sd transferred her previous knowledge of how to interpret the cue from a human, and used it with a conspecific.

Mason and Hollis's study (1962) found that rhesus monkeys were capable of using cues from conspecifics to find a hidden food reward. However, their subjects took hundreds of trials to learn to use the information from the conspecific. In this study, no monkey that learned to use a conspecific's cue did so in more than 190 trials. The authors also stated that while the body position of the cue-giver was important, there were probably other social cues that the subject was using to find the hidden reward. These results shed light on what types of cues capuchin monkeys could use to solve an object-choice task. While monkeys do not usually use gestures to communicate, they could learn to do so if the gesture was accompanied by other communicative information such

body position. Interestingly, Itakura et al. (1999) found that while chimpanzees could use a local enhancement cue (conspecific standing next to the food), they could not use a pointing cue from a conspecific. A probable cause for the differences was the distance between the conspecific and the reward location when the cue was given. The pointing cue was given when the chimpanzee was equidistant between the two buckets used in the task, while the local enhancement cue consisted of the chimpanzee standing directly next to the correct bucket. In this study, the apparatus was too small for the cueing monkeys to give their gestural cue from an equidistant position. Therefore, the subject monkey could have been reading the body position of the cueing monkey as well as the gesture. That being said, results showed that a gestural cue is necessary in order to solve this task, as Sc could not read any cues from Dv, who only gazed at the reward but did not reach for it.

Results also showed that capuchin monkeys were capable of learning to use a human pointing cue in fewer trials than previously thought. No monkey took more than 200 trials to reach criterion in any of the conditions. In a previous study (Anderson et al. 1995) the criteria for success was to obtain results significantly over chance (i.e. over 50% correct). Monkeys were given 270 trials to reach this criterion. The three animals tested reached criterion within the 270 trials, but only two ever got more than 80% correct in a block of 30 trials, and they each only did so in one or two blocks. Therefore since my criterion was to obtain 85% within a 20-trial block, in two consecutive blocks, and monkeys reached this criterion in 200 trials or less, they were more successful than capuchins in the previous study. Differences in performance between the two studies could have been a result of individual differences between the capuchin monkeys.

Results should be discussed within the context of perspective taking and Theory of Mind. Two aspects of Theory of Mind entail the understanding others' mental states, and that others' behavior is intentional (Tomasello & Call, 1997). The conspecific cue, given by another monkey, can be described as unintentional. The monkey was reaching towards the baited cup to retrieve the reward for itself and therefore, it was not doing so with the intention of signaling the subject monkey that the reward was in a particular cup. Rather, the subject monkey must have known that the cueing monkey was not telling it where to find the reward, but was trying to get the reward for itself. Therefore, it is possible that the subject monkey was taking the perspective of the cueing monkey and understanding its intention to grab the reward for itself. From this information, it would know which cup held the reward. However, there are a few reasons that this was probably not the case. First, it was more likely that the subjects were learning the reaching of the arm near the cup as an associative cue. They were simply choosing the cup that was nearest to the arm of the cueing monkey. This is a less cognitively complex mode of learning to solve this task, and does not require the subject to take the perspective or to understand the mental state of the cueing monkey. Secondly, if the subject monkey knew that there was always food in one of the cups, it might have recognized the physical actions of the cueing monkey towards the baited cup as one that was in some way similar to a 'food grabbing' action seen in their daily lives. It is possible the that subject monkey associated this movement with the location of food, and in that way understood that the cueing monkey was trying to get food in one of the cups; it should therefore choose that same cup, without having to take the mental perspective of

the cueing monkey. This explanation is consistent with the method capuchin monkeys use to find food. In this setting, they may often need to search for food in small holes, or retrieve food they have dropped in the cracks of different swings, perches, and toys that furnish their home cages. Monkeys can then learn that the methods others use to retrieve these pieces of food can signal the location of food. Thus, subjects may be recognizing an attempt to get to a reward, and choose the cup that was in the same direction in which the attempt was made. In this case they would be recognizing a behavioral cue and interpreting it for their own benefit, without needing to understand the mental state or intention of a conspecific. There is evidence that both apes and monkeys are capable of understanding that conspecifics are animate entities with their own goals and intentions. They can recognize individuals, predict the behaviors of others, formulate social strategies to manipulate the behavior of others, and learn from the behavior of others (Tomasello & Call, 1997). However, much of what is known about these cognitive abilities does not necessarily attribute Theory of Mind to nonhuman primates. There are many other explanations that could be given to some of these findings. For example, capuchin monkeys can understand that a conspecific had the goal of getting the food for itself, but not know what it was seeing, or have a mental representation of the visual perception of the other monkey.

The second cue was the pointing cue, sometimes accompanied by a vocalization, and was given by a human experimenter. The point differed from the conspecific cue in that it was intentional; the human experimenter was intentionally signaling to the subject the location of the food. However, the results of this study do not allow one to determine

if the subjects understood the mental state of the experimenter, or know what the experimenter saw. In all likelihood, they were learning to solve the task using simpler methods of associative cue learning. In their first trials, many subjects exhibited side-biases, in which they would continue to pick the same cup on every trial. This behavior could be explained by a lack of interest, a lack of understanding of what was required in the task, or the monkey not paying attention to the cue. However, most animals that exhibited a side bias eventually used the cue and switched to the other side, increasing success at the task. If the subject switched to the other cup and received a reward, they could have seen and associated the experimenter's finger on that same side. Therefore it was possible that witnessing the finger in proximity to the correct cup and then receiving a reward allowed the subjects to learn to always choose the cup that was in closest proximity to the experimenter's finger. However, that argument becomes weaker when one considers the time and repetition needed to train such a behavior in a capuchin monkey. Since many subjects spontaneously switched the cup they chose when they were exhibiting a side bias, and then immediately after increased their success, they only needed a few trials on which to learn that association. Therefore, the subject may not have learned to associate the finger with the closest cup, but instead learned (or was reminded) that there was the possibility of the reward being hidden in either of the cups as opposed to just one. At this point, the subject may have paid more attention to the cue giver to attempt to gather any information as to the whereabouts of the reward. The subject did not have to know what the experimenter saw, nor what they were thinking, to

understand that they were capable of giving them information about the location of the food.

This was the first study to document that capuchin monkeys can learn to use behavioral cues from conspecifics to solve an object choice task in a non-competitive environment. In addition, this study showed that they were also able to use their knowledge of how to interpret these cues in order to solve the same task when the cue giver was a human experimenter. This ability showed that they were flexible in their understanding of communicative skills in two ways. First, they interpreted cues of two different species for the same purpose. Second, they interpreted cues that were both intentional and unintentional. They may not have known whether a cue was intentional or not, but it may not matter depending on how they were learning to interpret the cues. If they were associating the closest arm or finger to the baited cup with a reward, the intentionality of the cue was irrelevant. The importance of these results was that capuchin monkeys were flexible in their learning of associating cues to find food, which could be an evolutionarily beneficial trait that can help them with foraging in the wild.

Interestingly, the two subjects that did not pass in any conditions were the alpha male (Mt) and alpha female (Sb) of the group. Such high-ranked animals should be able to succeed at this task since they are highly social and therefore may be more attuned to the movements of conspecifics. However, it is also possible that the alpha male and female were not as observant of lower-ranked animals during feeding times. They both have priority in the group when being fed, and as a result are usually the first to take the food. It is possible that they are not as motivated or as able as lower-ranked individuals

to learn strategies to gain food because higher-ranked individuals get rewards more often than others.

The individual differences exhibited by the subjects in this study provide evidence that individual capuchin monkeys interpret social cues in different ways. While six of the ten subjects were able to complete the task in conditions with a human given cue and a conspecific given cue, they all did so in different patterns, and within a different number of trials. Two of those subjects, Sd and Nk, could not initially learn the conspecific point, but were able to do so with a human when given the vocal point cue. The vocalization given with the point could have helped draw their attention to the task. In contrast, one subject, Sm, could not learn to use the human point, but was able to learn to use the conspecific cue within 80 trials. It is difficult to say which cue was objectively more obvious, because the point and the conspecific gesture were accompanied by other more subtle cues. The human point was accompanied by the gaze of the experimenter and sometimes by a vocalization, while the conspecific gestural cue was accompanied by the body position and gaze of the conspecific. It is possible that the human point was easier to learn as four out of the six successful subjects learned the human point first. However as there does not seem to be a pattern in the small sample size, I could not conclude that either cue was more obvious, or provided more information. The possibility of an order effect should also be analyzed to determine if the order of the type of cue givers that monkeys were given affected their performance. This is possible as two successful monkeys went from conspecific cueing to human pointing (Sc, Nw), while four went from human pointing to conspecific cueing (Sd, Nk, St, Ny). Further research could also

investigate why individual differences occur and how such differences affect our understanding of how nonhuman primates understand the behavioral cues of others.

Results showed that capuchin monkeys could learn to use gestural cues to solve an object-choice task even though monkeys do not use gestural communication in the wild. The ability to learn how to communicate the location of food, as well as to understand that another is intentionally communicating the location of food could be highly adaptive in foraging situations. More importantly, however, the ability to read the unintentional gestures of others to find food would require less complex cognition, and have the same result. Therefore, capuchin monkeys would benefit from the ability to read the body language of conspecifics in order to find food, or in other situations such as avoiding predators. Their apparent ability to learn these cues and then use them with humans shows that they are flexible, and could also have the ability to use cues from multiple individuals, or even from other species of monkeys.

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Tables

Table 1. Summary of Results For Subjects in all Conditions

Subject	**Group 1**	**C1**	**P1**	**VOC**	**P2**	**C2**
Sc	Conspecific-First	✓*	✓*			
Nw	Conspecific-First	✓*	✓*			
Sd	Conspecific-First	✓	✓	✓*	✓*	✓*
Nk	Conspecific-First	✓	✓	✓*	✓*	✓*
Mt	Conspecific-First	✓	✓	✓		
Subject	**Group 2**	**P1**	**C1**	**VOC**	**P2**	**C2**
St	Human-First	✓*	✓*			
Ny	Human-First	✓*	✓*			
Sm	Human-First	✓	✓*			
Dv	Human-First	✓	✓	✓*	✓*	✓
Sb	Human-First	✓	✓	✓		

Ten brown capuchin monkeys were randomly assigned into two groups, conspecific-first and human-first. Conditions are C1 (Conspecific 1), P1 (Pointing 1), VOC (Vocal), P2 (Pointing 2), and C2 (Conspecific 2). The order of conditions for each group varied. A check mark indicates the subject participated in the phase. An asterisk (*) indicates the criterion for success was reached in the condition, $p<.05$.

Figures

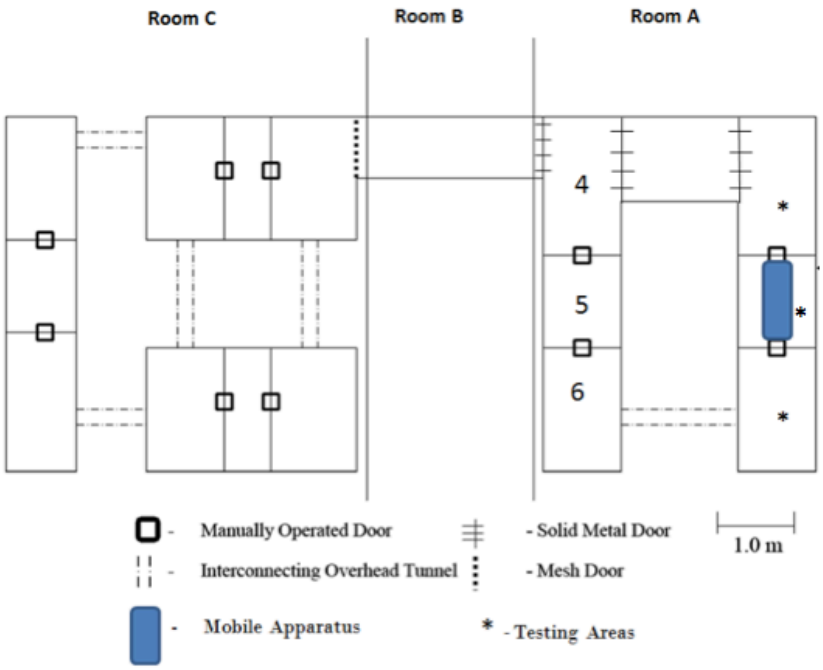
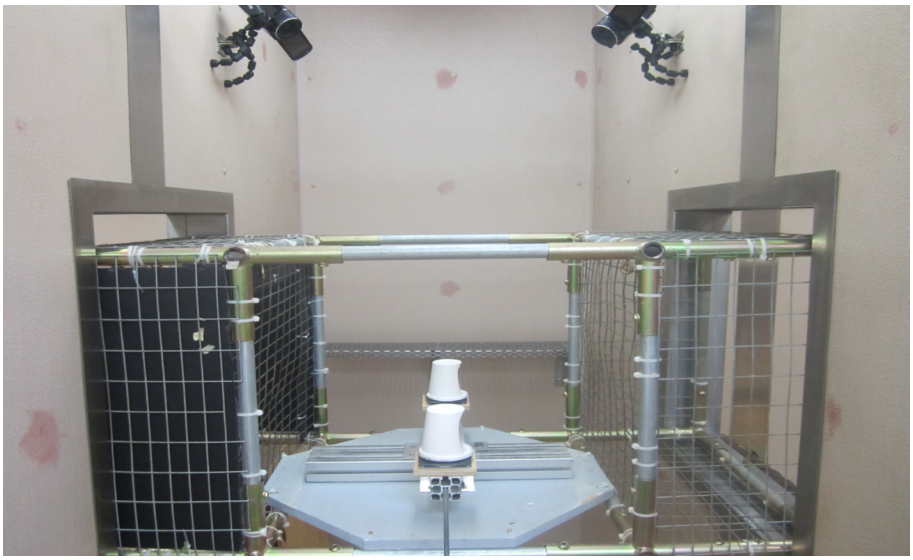


Figure 1. Diagram of entire enclosure. Testing chambers are indicated with asterisks and the location of the apparatus (adapted from Coyne, 2010)

(A)



(B)

(C)

Figure 2. Testing apparatus (A), trial with a human experimenter (B), and trial with a conspecific (C).

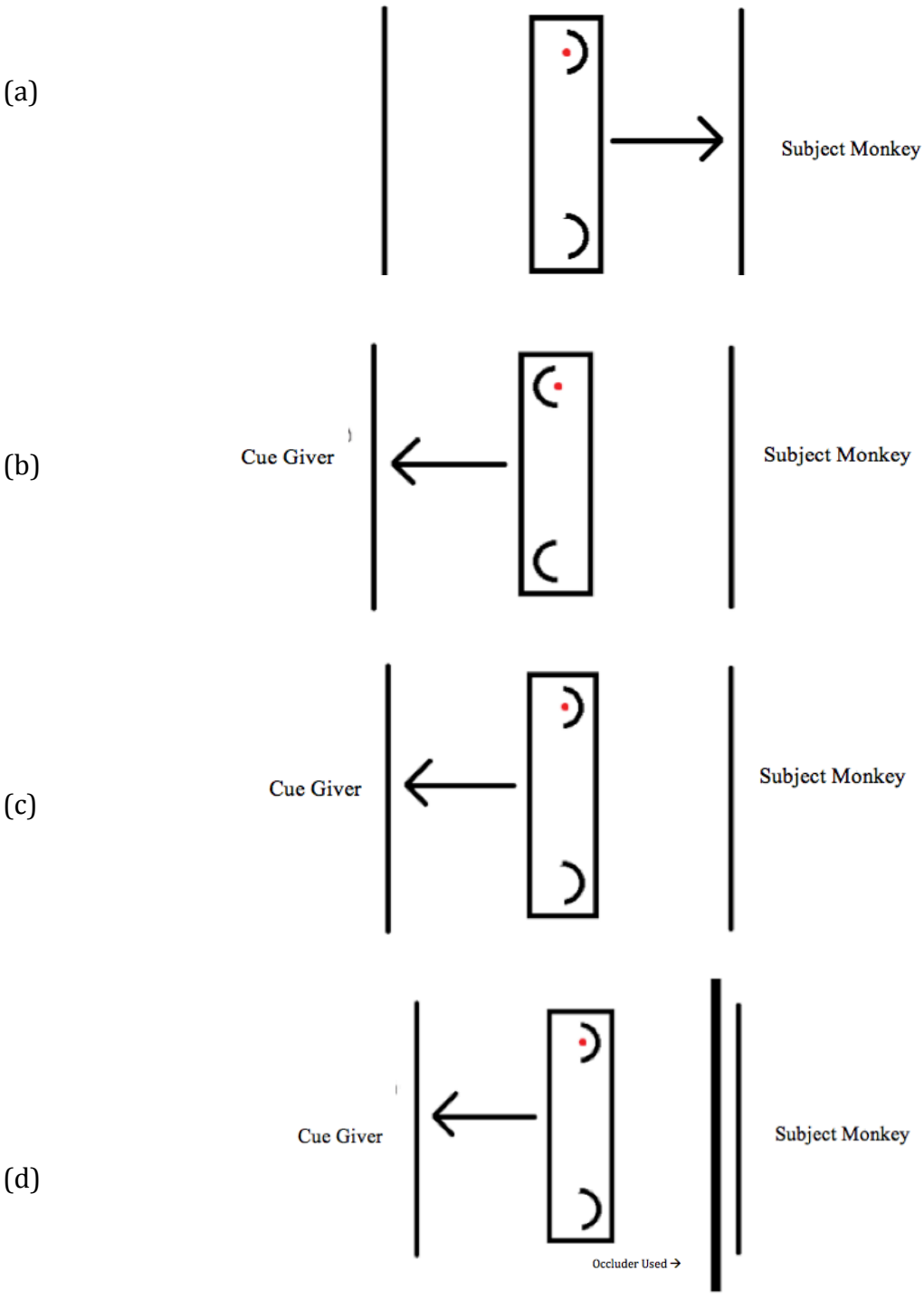


Figure 3. Diagrams of training phase 1 (a), phase 2 (b), phase 3 (c), and phase 4 (d).

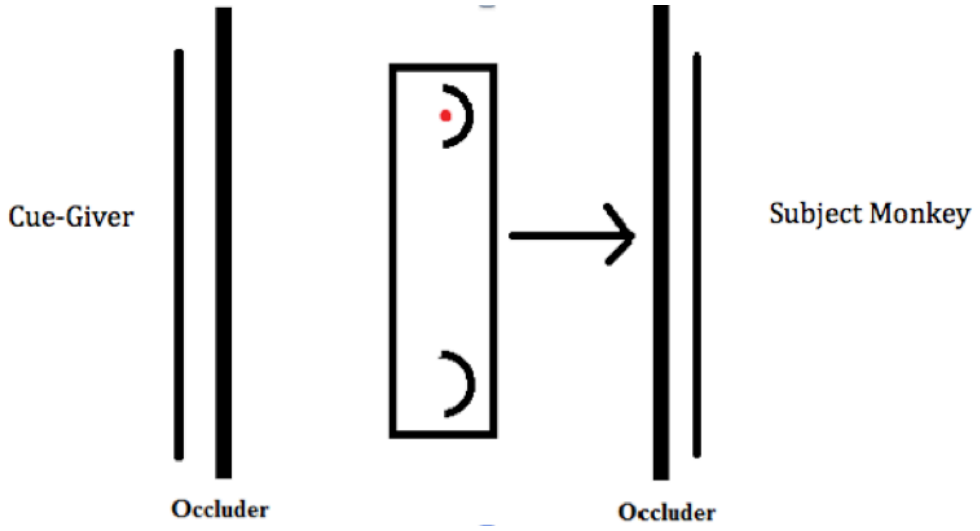


Figure 4. Diagram of test phase.

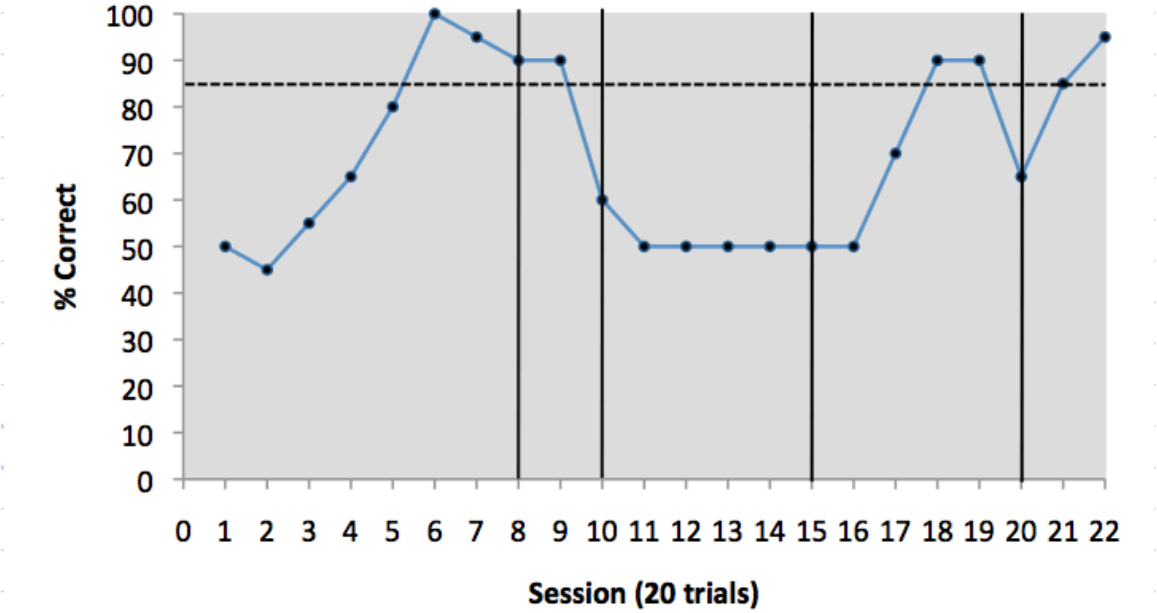


Figure 5. Percent correct for Sc over sessions of twenty trials. The dashed line indicates criterion for success (17/20 or 85%). The vertical lines indicate changes in cue giver from De, to Sd, to Dv, to Mt to a human.

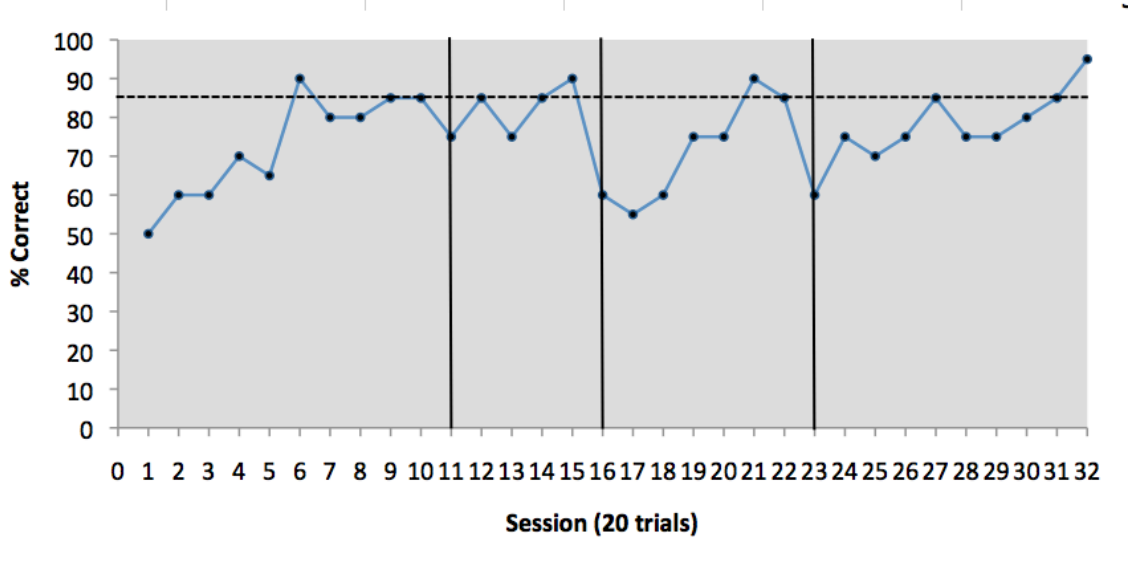


Figure 6. Percent correct for Nw over sessions of twenty trials. The dashed line indicates criterion for success (17/20 or 85%). The vertical lines indicate changes in cue giver from Sd, to Sc, to Mt to a human.

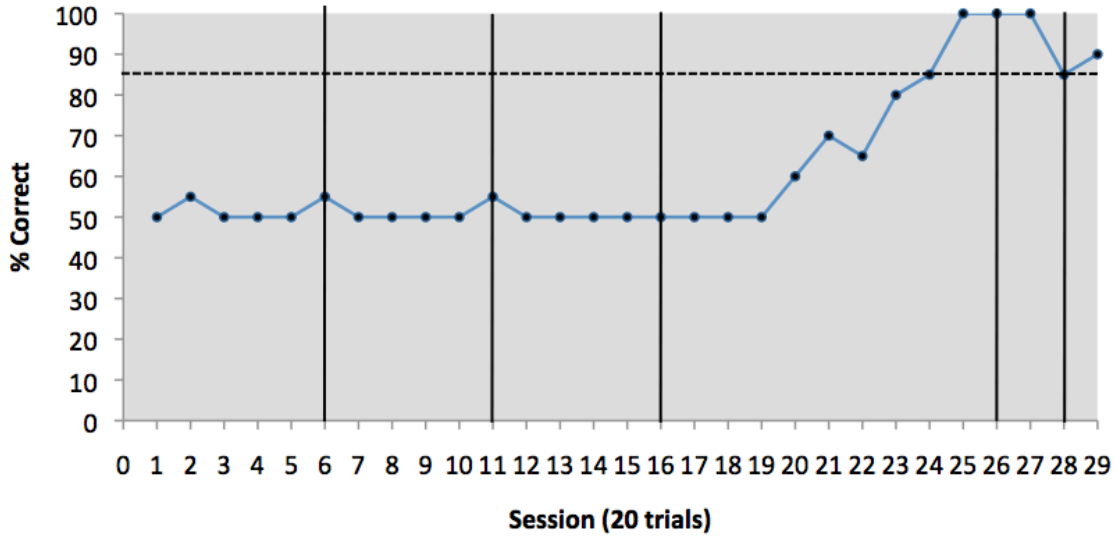


Figure 7. Percent correct for Sd over sessions of twenty trials. The dashed line indicates criterion for success (17/20 or 85%). The vertical lines indicate changes in cue giver from Sc, to Nk, to a human, to a human with a vocalization, to a human, to Sc.

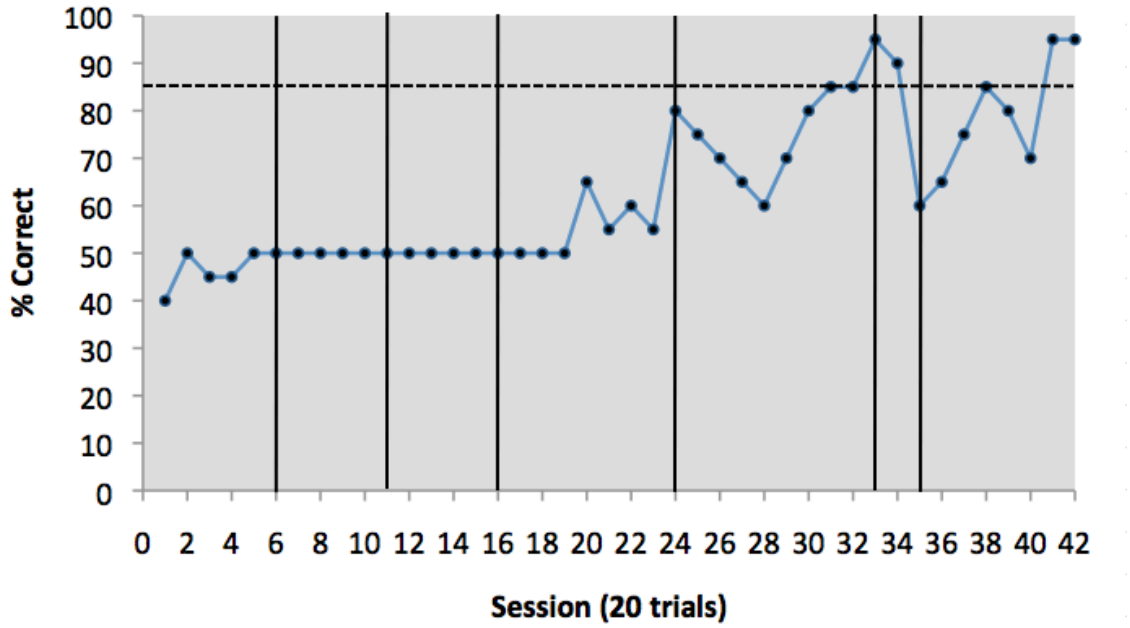


Figure 8. Percent correct for Nk over sessions of twenty trials. The dashed line indicates criterion for success (17/20 or 85%). The vertical lines indicate changes in cue giver from Nw, to Nb, to Sd, to a human, to a human with a vocalization, to a human, to Sd.

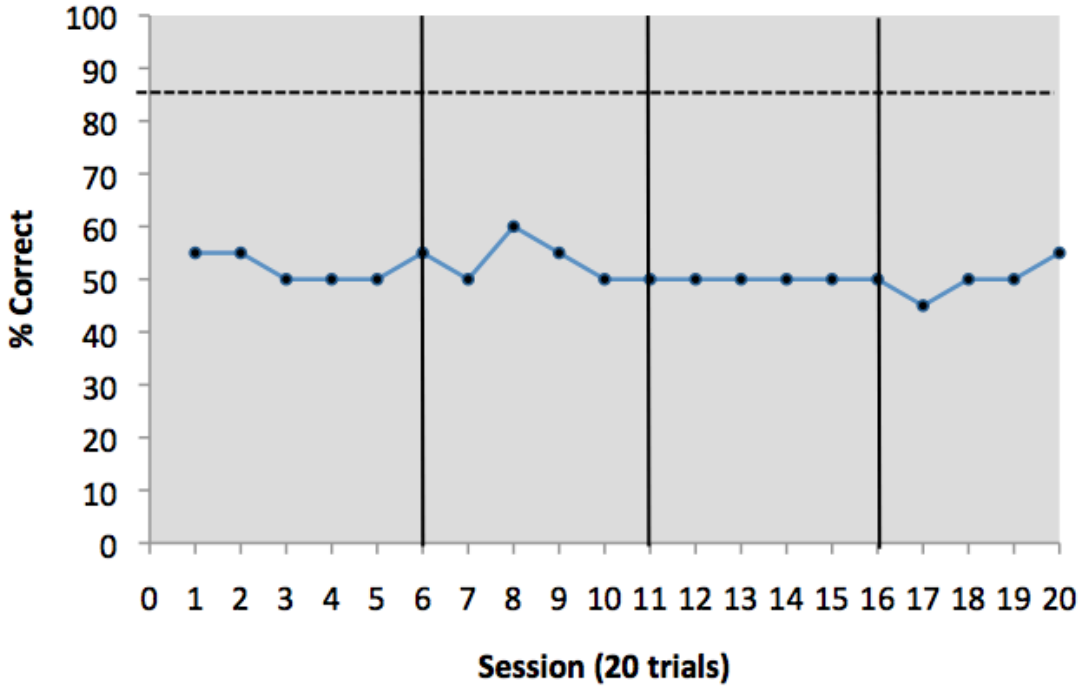


Figure 9. Percent correct for Mt over sessions of twenty trials. The dashed line indicates criterion for success (17/20 or 85%). The vertical lines indicate changes in cue giver from Nw, to Sd, to a human, to a human with a vocalization.

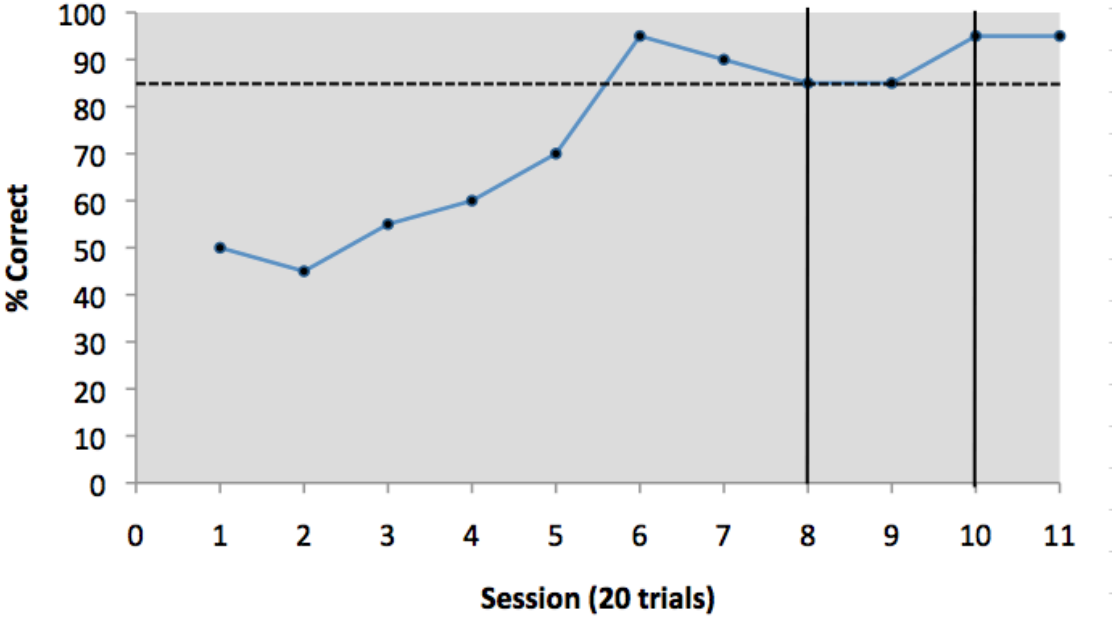


Figure 10. Percent correct for St over sessions of twenty trials. The dashed line indicates criterion for success (17/20 or 85%). The vertical lines indicate changes in cue giver from a human, to Ny, to Sc.

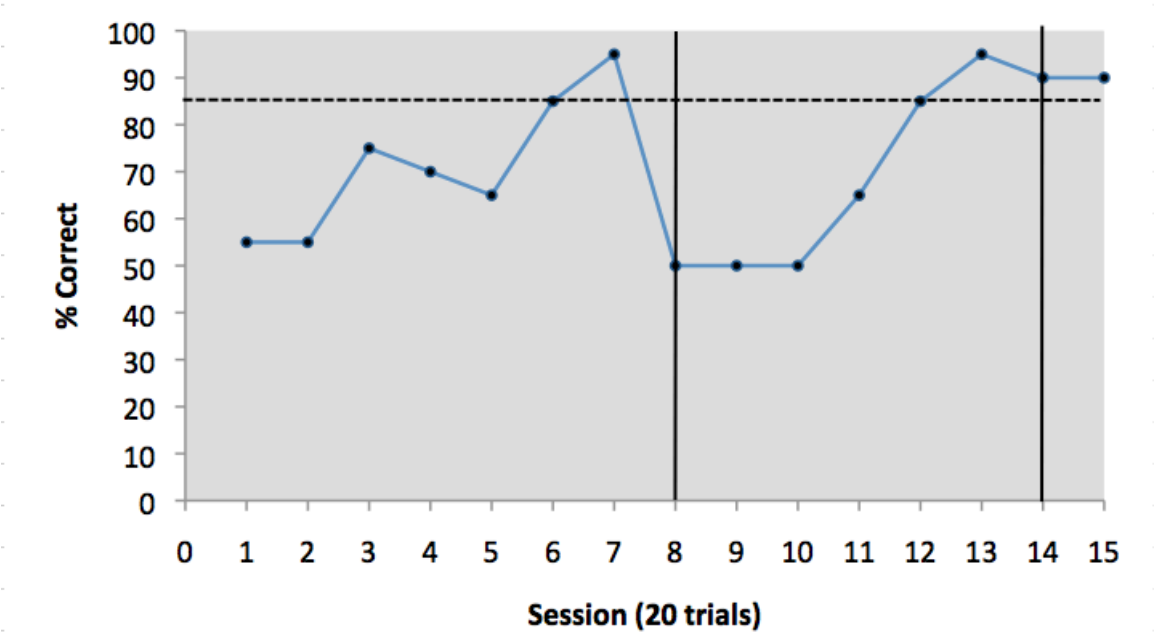


Figure 11. Percent correct for Ny over sessions of twenty trials. The dashed line indicates criterion for success (17/20 or 85%). The vertical lines indicate changes in cue giver from a human, to Sc, to Sd.

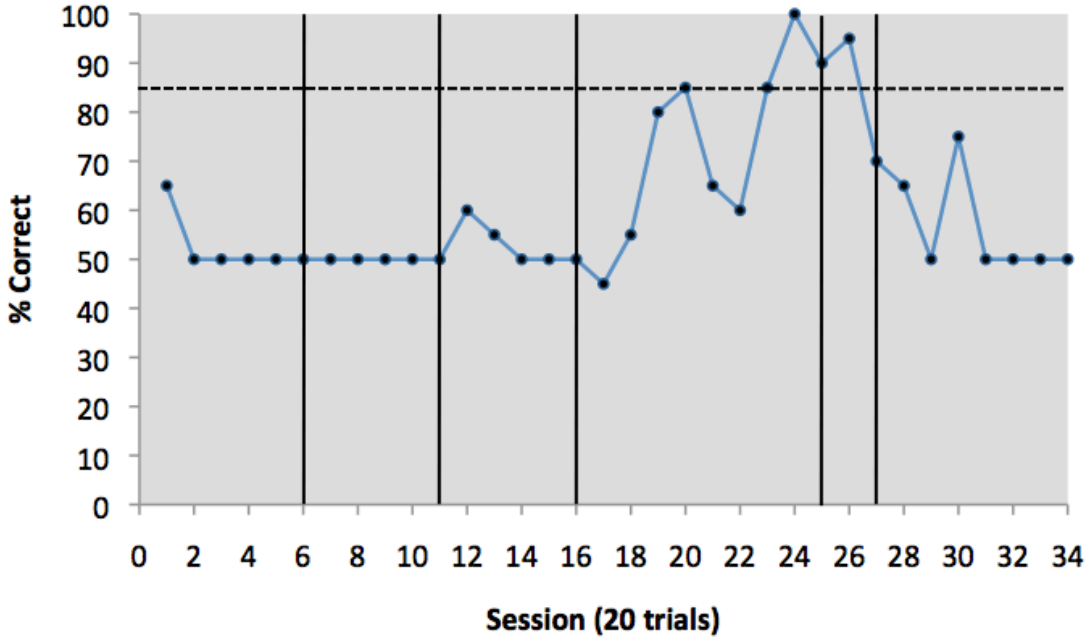


Figure 12. Percent correct for Dv over sessions of twenty trials. The dashed line indicates criterion for success (17/20 or 85%). The vertical lines indicate changes in cue giver from a human, to Sc, to Nw, to a human with a vocalization, to a human, to Sc.

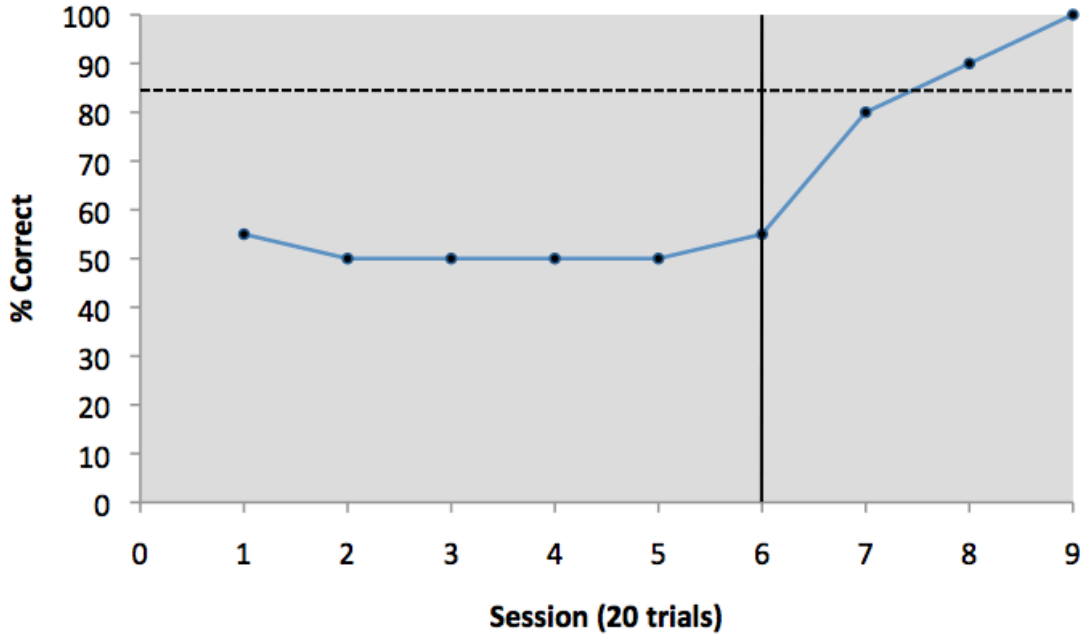


Figure 13. Percent correct for Sm over sessions of twenty trials. The dashed line indicates criterion for success (17/20 or 85%). The vertical lines indicate changes in cue giver from a human, to Ny.

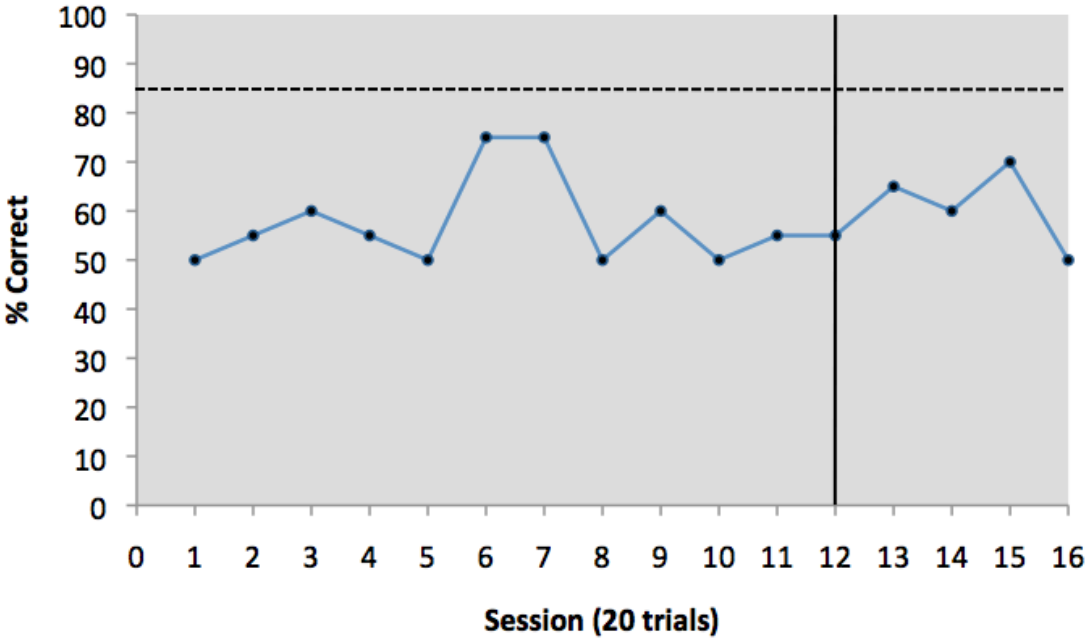


Figure 14. Percent correct for Sb over sessions of twenty trials. The dashed line indicates criterion for success (17/20 or 85%). The vertical lines indicate changes in cue giver from a human, to a human with vocalization.